

RESEARCH ARTICLE

Invasive alien Coypu (*Myocastor coypus*) as a prey of the native predator Eurasian Eagle Owl (*Bubo bubo*) in Bulgaria

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Received 4 January 2024 | Accepted 7 June 2024 | Published 31 December 2024

Citation: Milchev B, Spassov N (2024) Invasive alien Coypu (*Myocastor coypus*) as a prey of the native predator Eurasian Eagle Owl (*Bubo bubo*) in Bulgaria. Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 67(2): 443–462. <https://doi.org/10.3897/travaux.67.e118250>

Abstract

Incorporation of the invasive alien species into the food web by native predators is important both for managing the invasion and for predicting potential predator problems from measures taken against the invasive population. The present study of the Eurasian Eagle Owl (*Bubo bubo*) diet in the area designated as the initial centre for the introduction of the invasive Coypu (*Myocastor coypus*) in Bulgaria provided new data on the spread and reproduction of the invader. The small overlap in the distribution of the predator and the invader accounted for the small number of owl pairs with Coypu-containing diets. The long-term study confirmed the hunting of young Coypu by Eurasian Eagle Owls only in years with a very wide food niche of the predator in the respective territory. The occurrence of Coypu in the food of the owl did not depend on the frequency of other wetland inhabitants in the annual diets. The Coypu was incidental prey (range 0.5 – 0.8% by prey number) most likely due to the low density of the invader in the area of cohabitation with the predator.

Keywords

alien species, expanding distribution, predator-prey interaction, food web, pellet analyses.

Introduction

Invasive alien species, along with habitat destruction and alteration, are among the most important factors affecting biodiversity (Mack et al. 2000). The South American semi-aquatic rodent, the Coypu (*Myocastor coypus*) has been listed among the “World’s 100 worst invasive species” by IUCN (GISD 2023). Coypus have been introduced to all continents except Australia and Antarctica, usually with feral population from released animals from fur farms (Carter and Leonar 2002). The significant damage caused by this species results from its burrowing activity with weakening of dams and levees, fragmentation and destruction of wetland habitats by feeding on aquatic vegetation, and major impact on agriculture by feeding on crop plants (European Union 2020). The Coypu is a potential reservoir of dangerous infections for wild and domestic animals and humans (Zanzani et al. 2016; Križman et al. 2022). Coypu populations in EU Member States require targeted management to suppress population increases and to prevent further expansion under the EU Invasive Alien Species Regulation (1143/2014) (Smith et al. 2022).

The Coypu was introduced into two wetlands along the southern Black Sea coast of Bulgaria in 1953 (Peshev et al. 2004), but without subsequent targeted population surveys. The species was reported from a few isolated wetlands along the Black Sea coast until the year 2000 (Peshev et al. 2004), but Popov (2007) reduced these localities only to the proven ones in wetlands near the city of Burgas and at the mouth of the Batova River. These two locations are about 120 km away. The spike in reported new localities, mostly along the Maritza River and its tributaries in Central South Bulgaria, occurred just in the second decade of the current century (Gruychev 2012, 2017; Tsekova and Georgiev 2016; Mihaylov et al. 2017). Koshev et al. (2022) critically summarized the known data and presented many new localities in diverse wetlands throughout the country, but mostly up to 399 m a.s.l. in southern Bulgaria. Targeted displacement by people has contributed to this explosion in the species’ distribution after Koshev et al. (2022). Gruychev (2017) reported the only quantitative data for the Bulgarian population, which had a stable average density of 0.35 ind./km along the southernmost part of the Maritza River. There are no data on the reproduction and structure of the feral population in Bulgaria.

Alien species could diversely affect the guild of native predators for which they are potential prey (Carlsson et al. 2009; Speziale and Lambertucci 2013; Pintor and Byers 2015; David et al. 2017). Native predators might take advantage of the new, profitable prey (Barbar et al. 2016; Castillo-Ravanal et al. 2021; Olsson et al. 2021; Poli et al. 2022). Tracking the incorporation of the alien species into the food web by native predators is of particular interest in invasion study and management. Koshev et al. (2022) summarized data on single cases of Coypu predation by Red Fox (*Vulpes vulpes*) and Eastern Imperial Eagle (*Aquila heliaca*), but omitted predation by Eurasian Eagle Owls (*Bubo bubo*) in Bulgaria (Peshev et al. 2004; Milchev and Georgiev 2019). The Eurasian Eagle Owl is an opportunistic top predator with a preference for hunting mammals and birds weighing between 200 and 1900 g in a

variety of habitats (Penteriani and Delgado 2019; Scherzinger and Mebs 2020). Young Coypus fall into this weight group (Sherfy et al. 2006), and wetland inhabitants are among preferred prey of this owl species in Bulgaria (Milchev and Gruychev 2015; Milchev and Georgiev 2020). Analyses of local Eurasian Eagle Owl diets have already demonstrated the presence of wetland inhabitants with small threatened populations or secretive lifestyles (Miltshev and Sivkov 2006; Milchev and Menzel 2017).

This study adds to the knowledge about (i) the invasion and reproduction of Coypu and (ii) the new predator-prey relationship between the Eurasian Eagle Owl as one of the native threatened apex predators and the invasive Coypu as a potential alien prey.

Material and Methods

The study area covers about 10000 km² in south-eastern Bulgaria and includes the wetlands where the first introduction of Coypus occurred according to Peshev et al. (2004). Plain and hilly relief with open habitats prevails. Low mountains with ridges up to 300–400 m a.s.l. covered by broad-leaved forests dominated by oaks (*Quercus* spp.) are found along the border with Türkiye (see also Milchev and Menzel 2017). The climate is continental-mediterranean, characterized by hot and dry summers, mild winters and annual precipitation of up to 600–800 mm. The watershed between the Black and Aegean Seas bisects the area (Fig. 1). Smaller rivers and streams

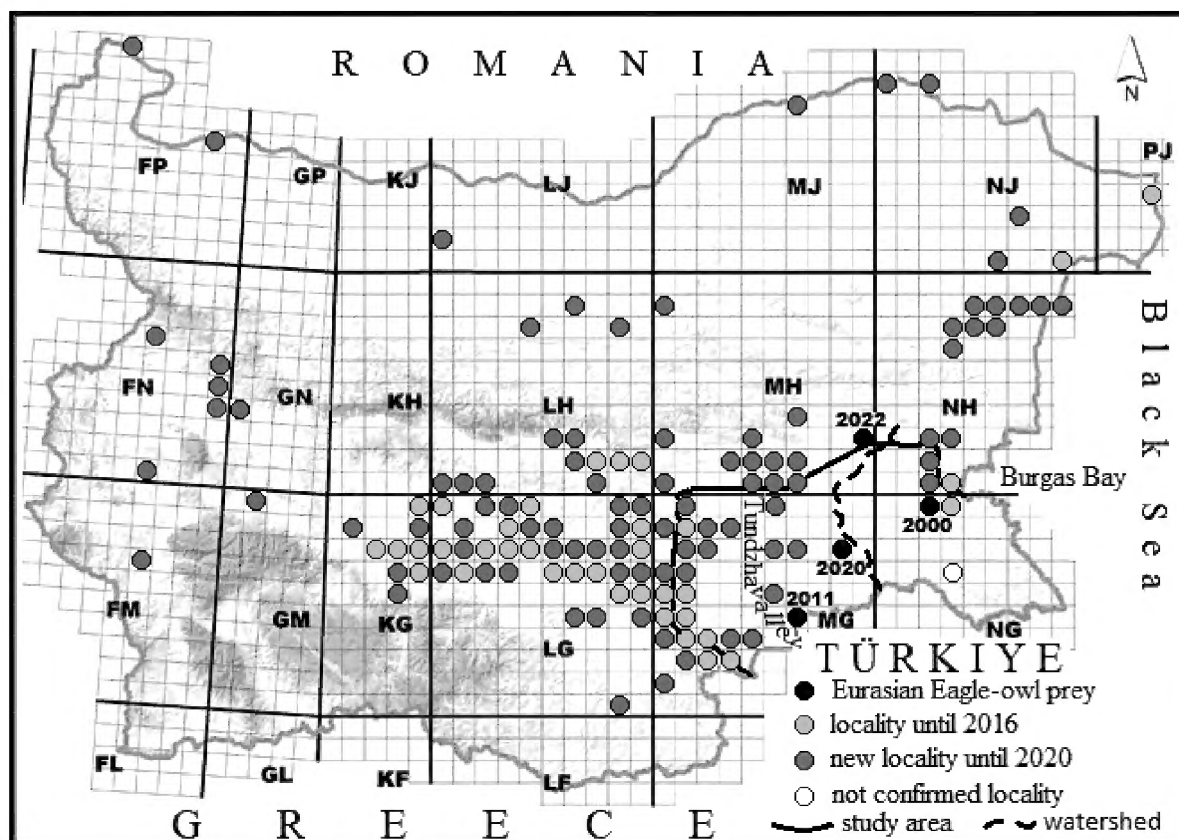


Figure 1. Distribution of Coypu (*Myocastor coypus*) in Bulgaria: localities recorded before 2016 according to Popov (2007), Gruychev (2017), Tsekova and Georgiev (2016) and Mihaylov et al. (2017); new localities between 2017–2020 after Koshev et al. (2022).

usually dry up in the summer, but numerous small, earth-walled dams retain water for irrigation, livestock watering, and fishponds. Bulrush (*Typha* sp.) and Common reed (*Phragmites australis*) communities grow in these artificial wetlands, but such aquatic vegetation is characteristic also for larger river valleys and coastal wetlands.

Data on the Coypu in Eurasian Eagle Owl diets have been collected during the analysis of food remains (pellets, parts of carcasses, etc.) from 53 Eurasian eagle owl-occupied rocky complexes in SE Bulgaria since 1994. The minimal evidences of an occupied rocky complex were food remains and excrements of Eurasian Eagle Owls. At least one fledgling per a brood, reaching the age of 45–50 days, determines breeding as successful. Older fledglings are hard to find because they tend to stray from the nest (Penteriani and Delgado 2019). Each successful nest was visited at least three times per year between April and September to collect prey remains. Prey species and minimal number of prey individuals in respective breeding locality/year were identified using the specialized literature for the respective prey group, comparative material from the National Museum of Natural History, Sofia (NMNHS), and the author's own comparative collection (see also Milchev and Georgiev 2019). Remains of a Coypu cranium with mandibles were determined according to Görne and Hackethal (1987) and submitted to Peshev et al. (2004). There was no comparative collection from Coypu pelvis and limb bones in NMNHS. Therefore, Milchev and Georgiev (2019) reported an uncertainly determined young individual. Pelvis and hind limb bones were extracted from a Coypu carcass found in a Eurasian Eagle Owl nest in 2022. The rest of the carcass was in the nest as food for the nestlings. These bones served to reliably identify materials collected in previous years (No. RM 1068, RM 1072 and RM 1073 in NMNHS collection).

Coypu distribution in Bulgaria was mapped on 10-km squares on the United Transverse Mercator grid based mainly on the generalized distribution according to Koshev et al. (2022). Coypus in owl diets were mapped in a square that included the main part of the respective Eurasian Eagle Owl hunting territory within a 2-km radius around occupied rocks (Penteriani and Delgado 2019). A concrete barrage with sluices supports a permanent water mirror on the Mochuritsa River (UTM square MH92). A Coypu was seen there and a young specimen was subsequently mapped there as a European eagle-owls prey. This owl hunting territory includes two small dams used for fish ponds in an adjacent square. These dams were dropped as Coypu habitats after an inspection and a negative response by tenant G. Rusev (pers. comm.) that the species had ever been present in them.

Tsekova and Georgiev (2016) and Koshev et al. (2022) reported Coypus in an isolated locality in the Tamna River in the Strandzha Mountains (UTM square NG36). The river almost dries up during the hotter summers and a series of pools up to 20–40 cm deep remain on the rocky and gravelly bottom. There are no muddy areas with hydrophytes (author's observations). Riparian forests of alder (*Alnus* spp.) and mountain ash (*Fraxinus excelsior*) form a green tunnel for the river (Dimitrov and Tashev 2015). Oak-dominated forests cover the narrow valley and surrounding hills. About 15 km of the course of the Tamna River were searched for signs of Coypu,

namely burrows, droppings and tracks (Salsamendi et al. 2009) on August 11 and 16, 2022.

The predictive models of Sherfy et al. (2006) were used to estimate age and weight from foot length of a Coypu carcass in a single Eurasian Eagle Owl nest. A gestation period of 130–134 days was deducted to retrospectively determine the conception period (Sherfy et al. 2006). The carcass was quite fresh, but without internal organs and abdominal wall, thus impossible to determine the sex. Female Coypus grow faster than males (Sherfy et al. 2006). Therefore, the predicted age and weight of this specimen were within a range that accounted for gender differences in growth.

The comparisons of annual diets (a breeding period diet/locality/successful year) within the Eurasian Eagle Owl localities with Coypu in the prey-list were based on the estimators: i) proportion (%) of other wetland inhabitants in annual diet: total number of wetland inhabitants divided by total prey number; ii) food niche breadth as computed: $FNB = 1/\sum p_i^2$, where p_i is the proportion of prey i by number in the annual diet (Levins 1968), here larger values indicate a higher dietary diversity; iii) dominant prey in the annual diet including Coypu: the two most numerous prey (%). We used Mann-Whitney U-test to compare the medians of FNB and proportions of wetland inhabitants between annual diets with/without Coypus, implemented with PAST 3.01 software (Hammer et al. 2001).

Results

Coypu distribution and reproduction

Invasive Coypus were evidenced with one predated young specimen each at four Eurasian Eagle Owl localities (Fig. 1, Table 1). Hereby we report the earliest finding of the Coypu in the Bulgarian part of the Tundzha River (MG64) and the first reproduction in tributaries of this river near the watershed between the Aegean and Black Seas. A locality of the invader was not confirmed by searching for Coypu in

Table 1. Diets of Eurasian Eagle Owls containing Coypu in Bulgaria: %N – percent by prey number (n) in an annual diet; FNB – food niche breadth.

UTM square (m a.s.l.)	Study period; successful owl breeding (occupations)	River; collection date	Coypu-containing diets		
			Wetland inhabitants %N	FNB	Dominant prey %N
NG29 (5 m)	1996 – 2022; 13 (27)	Sredetzka; 23.08.2000	27.1 n = 214	22.19	<i>Microtus arvalis/mystacinus</i> 10.7, <i>Gallinula chloropus</i> 7.5
MG64 (65 m)	1994 – 2013; 8 (18)	Tundzha; 23.08.2011	19.3 n = 202	17.14	<i>Erinaceus roumanicus</i> 15.8, <i>Microtus arvalis/mystacinus</i> 8.9
MG87 (150 m)	2005 – 2022; 12 (18)	Popovska; 29.05.2020	6.3 n = 126	20.67	<i>Microtus arvalis/mystacinus</i> 11.9, <i>Erinaceus roumanicus</i> 10.3
MH92 (160 m)	2008 – 2022; 5 (12)	Mochuritsa; 01.05.2022	19.0 n = 147	27.74	<i>Pelobates syriacus</i> 8.8, <i>Asio otus</i> 6.1

the Tamna River in square NG36 (Fig. 1). The species was observed only once when a Coypu swam across the Mochuritsa River in square MH92 on May 24, 2020. This observation was two years before the species was found as Eurasian Eagle Owl prey. The localities in squares MG64 and MH92 fall into Natura 2000 sites BG0002021 and BG0000196, respectively.

Coypu carcass remains in a Eurasian Eagle Owl nest in square MH92 were of a young individual aged 59–67 days weighing 800–900 g based on a foot length of 7.2 cm. It was born in the period February 22 – March 2, 2022, and conceived between October 11 and 23, 2021.

Predator-prey interactions

Coypu was found as a prey in 7.5% ($n = 53$) of the studied localities of Eurasian Eagle Owls and in 1.4% ($n = 285$) of the diets of successful breeding pairs. The predation occurred in 25% ($n = 8$ squares) of the predator-prey coexistence squares. The invader ranged between 0.5 – 0.8% (average $0.63\% \pm 0.15$) by prey number in the four Coypu-containing diets (Table 2). Coypus accounted for 0.05% ($n = 8013$ prey specimens, Table 3) of total prey in annual diets ($n = 38$ diets) at the four Eurasian Eagle Owl localities.

The occurrence of Coypu in the prey list did not depend on the proportion of wetland inhabitants in the predator's annual diet ($n = 38$ diets) in the four localities (average $18.0\% \pm 8.6$ wetland inhabitants, range 6.3 – 27.1%; Fig. 2). The difference between the medians of the proportions of wetland inhabitants in annual diets with and without a Coypu were nonsignificant ($U = 51$, $z = -0.78$, $P > 0.05$, Mann-Whitney U-test). A single diet hosted wetland inhabiting species as dominant prey, the Common Moorhen (*Gallinula chloropus*) was numerically predominant in a Coypu-containing diet (Table 1).

Eurasian Eagle Owls preyed on Coypu only in years with very wide food niches (FNB, average 21.94 ± 4.41 , range 17.14 – 27.74; Table 1, Fig. 2). There was a statistically highly significant difference between the median FNB of annual diets with and without an invader at the four localities ($U = 9$, $z = -2.78$, $P < 0.01$).

Discussion

Coypu distribution and reproduction

The modern distribution of the Coypu in the central and eastern part of southern Bulgaria (Koshev et al. 2022) could not be explained by a population explosion and displacement from the only confirmed location along the Black Sea coast near the city of Burgas until 2000 (Peshev et al. 2004; Popov 2007). Coypu-preferred wetlands with slow-flowing or standing water and overgrowth of hydrophytes (Carter and Leonar 2002; Cocchi and Riga 2008) to the west of this site, around and south of Burgas Bay were unoccupied. In fact, the seashore should help the spread of the Coypu as reported by Stille et al. (2021) on the Greek island of Corfu. Koshev et al. (2022) left

Table 2. Eurasian Eagle Owl diets containing Coypus in four breeding territories (UTM squares) in Bulgaria: N – number of prey specimens; % N - % by number.

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N
<i>Talpa europaea</i>	1	0,5	1	0,5			1	0,7
<i>Crocidura leucodon</i>							1	0,7
<i>Crocidura suaveolens</i>							1	0,7
<i>Erinaceus roumanicus</i>	5	2,3	32	15,8	13	10	5	3,4
<i>Lepus europaeus</i>	6	2,8	5	2,5	6	4,8	5	3,4
<i>Spermophilus citellus</i>							1	0,7
<i>Myocastor coypus</i>	1	0,5	1	0,5	1	0,8	1	0,7
<i>Glis glis</i>			1	0,5	2	1,6		
<i>Dryomys nitedula</i>					1	0,8		
<i>Microtus arvalis/mystacinus</i>	23	10,7	18	8,9	15	12	7	4,8
<i>Microtus hartingi</i>					9	7,1		
<i>Microtus subterraneus</i>	1	0,5						
<i>Arvicola amphibius</i>	14	8,5	3	1,5	1	0,8	5	3,4
<i>Apodemus flavicollis/sylvaticus</i>	5	2,3	14	8,9	8	4,8	3	2,0
<i>Apodemus agrarius</i>	1	0,5						
<i>Rattus rattus</i>	2	0,9	4	2,0	5	4,0		
<i>Rattus norvegicus</i>	21	9,8			2	1,6	2	1,4
<i>Mus musculus/macedonicus</i>	4	1,9	2	1,0	3	2,4	8	5,4
<i>Nannospalax leucodon</i>			2	1,0				
<i>Vulpes vulpes</i>			1	0,5				
<i>Mustela nivalis</i>							1	0,7
Mammalia subtotal	84	39,3	84	41,6	64	51	41	28
<i>Coturnix coturnix</i>	2	0,9	8	4,0	1	0,8	1	0,7
<i>Phasianus colchicus</i>							2	1,4
<i>Perdix perdix</i>	4	1,9	5	2,5	5	4,0	8	5,4
<i>Gallus gallus dom.</i>	1	0,5						
<i>Aythya ferina</i>	1	0,5						
<i>Aythya nyroca</i>							1	0,7
<i>Spatula querquedula</i>	1	0,5					1	0,7
<i>Spatula clypeata</i>	1	0,5						
<i>Anas platyrhynchos</i>	2	0,9			1	0,8	1	0,7
<i>Anas sp.</i>	2	0,9						
<i>Tachybaptus ruficollis</i>	1	0,5	6	3,0			1	0,7
<i>Columba livia f. dom.</i>			1	0,5	4	3,2		
<i>Columba palumbus</i>			1	0,5	5	4,0	3	2,0
<i>Streptopelia turtur</i>	3	1,4			3	2,4	3	2,0
<i>Streptopelia decaocto</i>			2	1,0	2	1,6	4	2,7
<i>Rallus aquaticus</i>	2	0,9					2	1,4
<i>Crex crex</i>	1	0,5	3	1,5			1	0,7
<i>Zapornia parva</i>			2	1,0				
<i>Zapornia parva/pusilla</i>							1	0,7
<i>Gallinula chloropus</i>	16	7,5	15	7,4	2	1,6	6	4,1
<i>Fulica atra</i>	5	2,3	1	0,5	1	0,8	2	1,4
<i>Ixobrychus minutus</i>	1	0,5	4	2,0	1	0,8	2	1,4
<i>Nycticorax nycticorax</i>	2	0,9			1	0,8		

Table 2. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N
<i>Ardeola ralloides</i>	2	0,9						
<i>Ardea purpurea</i>							2	1,4
<i>Vanellus vanellus</i>	4	1,9						
<i>Scolopax rusticola</i>			2	1,0	1	0,8	2	1,4
<i>Larus ridibundus</i>	1	0,5						
<i>Chlidonias niger</i>	1	0,5						
<i>Tyto alba</i>	1	0,5			2	1,6		
<i>Athene noctua</i>					4	3,2	3	2,0
<i>Otus scops</i>	2	0,9	1	0,5	2	1,6	5	3,4
<i>Asio otus</i>	1	0,5	3	1,5	4	3,2	9	6,1
<i>Circus pygargus</i>					1	0,8		
<i>Circus sp.</i>			1	0,5				
<i>Accipiter nisus</i>			2	1,0	1	0,8	2	1,4
<i>Buteo buteo</i>	2	0,9	1	0,5			1	0,7
<i>Merops apiaster</i>	1	0,5	1	0,5				
<i>Coracias garrulus</i>	1	0,5	2	1,0				
<i>Picus viridis</i>					1	0,8		
<i>Falco tinnunculus</i>	2	0,9	1	0,5			1	0,7
<i>Lanius collurio</i>	3	1,4	1	0,5	1	0,8		
<i>Lanius minor</i>							1	0,7
<i>Garrulus glandarius</i>	4	1,9			2	1,6		
<i>Pica pica</i>	8	3,7	2	1,0	2	1,6	3	2,0
<i>Corvus monedula</i>	2	0,9						
<i>Corvus corone</i>	1	0,5			1	0,8	1	0,7
<i>Oriolus oriolus</i>	1	0,5						
<i>Melanocorypha calandra</i>			6	3,0				
<i>Galerida cristata</i>	1	0,5						
<i>Lullula arborea</i>	1	0,5						
<i>Alauda arvensis</i>	1	0,5	3	1,5				
<i>Sylvia sp.</i>	1	0,5						
<i>Sturnus vulgaris</i>	1	0,5			1	0,8	2	1,4
<i>Pastor roseus</i>	4	1,9						
<i>Turdus merula</i>			5	2,5	2	1,6	3	2,0
<i>Turdus philomelos</i>	5	2,3	5	2,5	3	2,4	7	4,8
<i>Turdus sp.</i>	1	0,5	1	0,5				
<i>Coccothraustes coccothraustes</i>	1	0,5						
<i>Emberiza calandra</i>	2	0,9	2	1,0			1	0,7
<i>Emberiza sp.</i>					1	0,8		
Passeriformes indet.			1	0,5	5	4		
Aves subtotal	100	46,7	88	43,6	60	48	82	55,8
<i>Natrix natrix</i>			1	0,5				
Reptilia subtotal			1	0,5				
<i>Pelobates syriacus</i>	9	4,2	14	6,9	1	0,8	13	8,8
<i>Pelophylax ridibundus</i>			5	2,5				
Amphibia subtotal	9	4,2	19	9,4	1	0,8	13	8,8
<i>Potamon ibericum</i>	1	0,5						

Table 2. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N
<i>Pontastacus leptodactylus</i>							3	2,0
<i>Scolopendra</i> sp.			1	0,5				
<i>Decticus albifrons</i>			4	2,0			3	2,0
<i>Decticus albifrons/verrucivorus</i>	1	0,5						
<i>Platycleis escaleraei/intermedia</i>							5	3,4
<i>Gryllotalpa</i> cf. <i>stepposa</i>	13	6,1	1	0,5				
<i>Cerambyx</i> sp.	3	1,4	4	2,0	1	0,8		
<i>Lucanus cervus</i>	3	1,4						
Invertebrates subtotal	21	9,8	10	5,0	1	0,8	11	7,5
Total	214	100	202	100	126	100	147	100

a Coypu-free strip over 50 km wide around the watershed between the catchment areas of the Black and Aegean seas. Two Eurasian Eagle Owl localities with Coypu-containing diets fell within this strip, but the mountainous, forested terrain east of square MG87 had no potential for Coypu dispersal. Slanting slopes with arable land and pastures at a minimum of about 180 m a.s.l. or only 20 m above the new locality of the invader in square MH92 were present around the watershed and to the east to the Coypu localities in the Black Sea catchment area noted by Koshev et al. (2022). Here, contact between the Coypu populations near the Burgas Bay and in the Tundzha valley with its tributaries would be possible. This would hardly led to the expansion of Coypus in the Tundzha and Maritza rivers with their tributaries according to data from the invasion in neighboring Türkiye and our owl diet results. The Maritza River (Meriç in Türkiye) receives the waters of the Tundzha (Tunja) River in Türkiye and flows as a border river between Greece and Türkiye towards the Aegean Sea. The first Coypu most likely of Bulgarian origin was found in the Maritza/Meriç River in Türkiye in 1984, and there were ten localities with the invader by 1997 (Özkan and Kurtonur 1994; Özkan 1999). One of these localities was in Tundzha River with one individual each in 1989 and 1997, where Özkan (1999) considered the species rare. This locality is only about 20 km from the first known one in the Bulgarian section of the Tundzha River in the square MG64. Subsequent reports from the Tundzha Valley and its tributaries in Bulgaria (present study; Koshev et al. 2022) rather confirmed down to upstream spread of the Coypu from Türkiye. The widespread distribution of the Coypu in central southern Bulgaria during the last decade rather reflected a better level of knowledge of the population status with several unknown centers of spreading than an expansion from the initial, single known introduction area near Burgas Bay.

Coypus breed throughout the year, but data on the reproductive peculiarities of local populations are critical to organize effective management of the invader (Sherfy et al. 2006; Cocchi and Riga 2008; Lori et al 2013). Retrospectively determined birth and conception periods of a single prey individual of Eurasian Eagle Owls coincided

Table 3. Total Eurasian Eagle Owl diets in four breeding territories (UTM squares) containing Coypus in Bulgaria: N – number of prey specimens; % N - % by number.

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N	Total N	% N
<i>Talpa europaea</i>	14	0,4	13	0,8	6	0,3	5	0,5	38	0,5
<i>Talpa martinorum</i>	2	0,1							2	0,02
<i>Crocidura leucodon</i>	8	0,2	1	0,1	5	0,2	1	0,1	15	0,2
<i>Crocidura suaveolens</i>	9	0,3	1	0,1	7	0,3	1	0,1	18	0,2
<i>Neomys anomalus</i>	1	0,03							1	0,01
<i>Erinaceus roumanicus</i>	148	4,5	153	9,8	242	11,0	64	6,4	607	7,6
<i>Myotis capaccinii</i>	1	0,03							1	0,01
<i>Vespertilionidae</i>	1	0,03			1	0,05			2	0,02
<i>Lepus capensis</i>	73	2,2	52	3,3	64	2,9	22	2,2	211	2,6
<i>Spermophilus citellus</i>	18	0,6	1	0,1	1	0,05	4	0,4	24	0,3
<i>Myocastor coypus</i>	1	0,03	1	0,1	1	0,05	1	0,1	4	0,05
<i>Cricetulus migratorius</i>							1	0,1	1	0,01
<i>Glis glis</i>	1	0,03	1	0,1	3	0,1			5	0,06
<i>Dryomys nitedula</i>	1	0,03			4	0,2			5	0,06
<i>Microtus arvalis/mystacinus</i>	1002	30,7	271	17,4	393	17,9	97	9,7	1763	22,0
<i>Microtus hartingi</i>	6	0,2	1	0,1	267	12,2			274	3,4
<i>Microtus subterraneus</i>	6	0,2			1	0,05			7	0,1
<i>Arvicola terrestris</i>	125	3,8	45	2,9	19	0,9	40	4,0	229	2,9
<i>Apodemus flavicollis/sylvaticus</i>	276	8,5	55	3,5	104	4,7	83	8,3	518	6,5
<i>Apodemus agrarius</i>	1	0,03							1	0,01
<i>Rattus rattus</i>	23	0,7	26	1,7	45	2,1			94	1,2
<i>Rattus norvegicus</i>	177	5,4	2	0,1	160	7,3	49	4,9	388	4,8
<i>Mus musculus/macedonicus</i>	106	3,2	13	0,8	64	2,9	58	5,8	241	3,0
<i>Nannospalax leucodon</i>	4	0,1	15	1,0	3	0,1	3	0,3	25	0,3
<i>Vulpes vulpes</i>	5	0,2	9	0,6	1	0,05	1	0,1	16	0,2
<i>Mustela nivalis</i>	3	0,1			9	0,4	2	0,2	14	0,2
Mammalia subtotal	2012	61,6	660	42,5	1400	63,8	432	43,2	4504	56,2
<i>Coturnix coturnix</i>	18	0,6	37	2,4	23	1,0	20	2,0	98	1,2
<i>Alectoris chukar</i>			3	0,2					3	0,04
<i>Phasianus colchicus</i>							2	0,2	2	0,02
<i>Perdix perdix</i>	14	0,4	41	2,6	38	1,7	41	4,1	134	1,7
<i>Gallus gallus dom.</i>	1	0,03	1	0,1	1	0,05			3	0,04
<i>Aythya ferina</i>	1	0,03							1	0,01
<i>Aythya nyroca</i>	1	0,03					1	0,1	2	0,02
<i>Aythya sp.</i>	1	0,03							1	0,01
<i>Spatula querquedula</i>	24	0,7	2	0,1	4	0,2	3	0,3	33	0,4
<i>Spatula clypeata</i>	11	0,3							11	0,1
<i>Mareca strepera</i>	2	0,1							2	0,02
<i>Anas platyrhynchos</i>	15	0,5	6	0,4	12	0,5	3	0,3	36	0,4
<i>Anas crecca</i>	2	0,1			1	0,05			3	0,04
<i>Anas crecca/Spatula querquedula</i>	6	0,2	2	0,1			2	0,2	10	0,1
<i>Anas sp.</i>	10	0,3							10	0,1
<i>Tachybaptus ruficollis</i>	24	0,7	21	1,4	3	0,1	2	0,2	50	0,6
<i>Podiceps cristatus</i>	4	0,1			1	0,05			5	0,1
<i>Columba livia f. dom.</i>	19	0,6	6	0,4	15	0,7	7	0,7	47	0,6

Table 3. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N	Total N	% N
<i>Columba palumbus</i>	12	0,4	2	0,1	30	1,4	10	1,0	54	0,7
<i>Streptopelia turtur</i>	7	0,2	10	0,6	5	0,2	12	1,2	34	0,4
<i>Streptopelia decaocto</i>	7	0,2	17	1,1	4	0,2	6	0,6	34	0,4
<i>Caprimulgus europaeus</i>			1	0,1	1	0,05			2	0,02
<i>Cuculus canorus</i>	3	0,1	4	0,3			5	0,5	12	0,1
<i>Rallus aquaticus</i>	34	1,0	7	0,5	2	0,1	6	0,6	49	0,6
<i>Crex crex</i>	32	1,0	18	1,2	5	0,2	19	1,9	74	0,9
<i>Porzana porzana</i>	10	0,3	2	0,1					12	0,1
<i>Zapornia parva</i>	9	0,3	3	0,2	1	0,05	2	0,2	15	0,2
<i>Zapornia pusilla</i>	1	0,03					1	0,1	2	0,02
<i>Zapornia parva/pusilla</i>							1	0,1	1	0,01
<i>Gallinula chloropus</i>	104	3,2	56	3,6	49	2,2	47	4,7	256	3,2
<i>Fulica atra</i>	57	1,7	15	1,0	11	0,5	14	1,4	97	1,2
<i>Botaurus stellaris</i>	2	0,1	1	0,1					3	0,04
<i>Ixobrychus minutus</i>	10	0,3	16	1,0	14	0,6	15	1,5	55	0,7
<i>Nycticorax nycticorax</i>	25	0,8	2	0,1	9	0,4	1	0,1	37	0,5
<i>Ardeola ralloides</i>	4	0,1							4	0,05
<i>Ardea purpurea</i>							2	0,2	2	0,02
<i>Microcarbo pygmaeus</i>			1	0,1	4	0,2			5	0,1
<i>Recurvirostra avosetta</i>					1	0,05			1	0,01
<i>Himantopus himantopus</i>	2	0,1							2	0,02
<i>Pluvialis apricaria</i>	1	0,03							1	0,01
<i>Vanellus vanellus</i>	31	0,9					4	0,4	35	0,4
<i>Charadriidae gen.</i>	1	0,03	1	0,1					2	0,02
<i>Numenius/Limosa</i>	1	0,03							1	0,01
<i>Calidris pugnax</i>	2	0,1					1	0,1	3	0,04
<i>Calidris minuta</i>	1	0,03							1	0,01
<i>Calidris minuta/temminckii</i>	1	0,03							1	0,01
<i>Tringa ochropus</i>	2	0,1	1	0,1					3	0,04
<i>Tringa nebularia</i>	1	0,03							1	0,01
<i>Tringa sp.</i>	3	0,1							3	0,04
<i>Scolopax rusticola</i>	11	0,3	9	0,6	20	0,9	3	0,3	43	0,5
<i>Gallinago gallinago</i>	1	0,03	1	0,1					2	0,02
<i>Scolopacidae gen.</i>	2	0,1	1	0,1					3	0,04
<i>Larus cachinnans/michahellis</i>	2	0,1					1	0,1	3	0,04
<i>Larus melanocephalus</i>					1	0,05			1	0,01
<i>Larus ridibundus</i>	4	0,1			1	0,05			5	0,1
<i>Chlidonias niger</i>	1	0,03							1	0,01
<i>Charadriiformes indet.</i>			1	0,1					1	0,01
<i>Tyto alba</i>	41	1,3	4	0,3	38	1,7	8	0,8	91	1,1
<i>Athene noctua</i>	32	1,0	15	1,0	12	0,5	4	0,4	63	0,8
<i>Otus scops</i>	17	0,5	7	0,5	13	0,6	6	0,6	43	0,5
<i>Asio otus</i>	52	1,6	32	2,1	46	2,1	24	2,4	154	1,9
<i>Asio flammeus</i>					4	0,2			4	0,05
<i>Strix aluco</i>	2	0,1							2	0,02
<i>Bubo bubo</i>	3	0,1	1	0,1			1	0,1	5	0,1

Table 3. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N	Total N	% N
<i>Pernis apivorus</i>	1	0,03							1	0,01
<i>Circus aeruginosus</i>	1	0,03							1	0,01
<i>Circus cyaneus</i>					1	0,05			1	0,01
<i>Circus pygargus</i>	1	0,03			1	0,05	1	0,1	3	0,04
<i>Circus</i> sp.			2	0,1					2	0,02
<i>Accipiter nisus</i>	2	0,1	3	0,2	2	0,1	3	0,3	10	0,1
<i>Accipiter brevipes</i>					1	0,05			1	0,01
<i>Accipiter gentilis</i>			3	0,2	2	0,1			5	0,06
<i>Buteo buteo</i>	12	0,4	9	0,6	29	1,3	1	0,1	51	0,6
<i>Buteo rufinus</i>	1	0,03					2	0,2	3	0,04
<i>Merops apiaster</i>	4	0,1	1	0,1	1	0,05			6	0,1
<i>Coracias garrulus</i>	1	0,03	3	0,2			1	0,1	5	0,1
<i>Alcedo atthis</i>	1	0,03							1	0,01
Alcedinidae gen.			1	0,1					1	0,01
<i>Upupa epops</i>	3	0,1	1	0,1					4	0,05
<i>Jynx torquilla</i>	2	0,1	1	0,1					3	0,04
<i>Picus viridis</i>					2	0,1			2	0,02
<i>Leiopicus medius</i>	1	0,03					1	0,1	2	0,02
<i>Dendrocopos major</i>	2	0,1							2	0,02
<i>Falco tinnunculus</i>	15	0,5	4	0,3	1	0,05	9	0,9	29	0,4
<i>Falco subbuteo</i>	1	0,03	1	0,1					2	0,02
<i>Falco cherrug</i>					1	0,05			1	0,01
<i>Lanius collurio</i>	33	1,0	8	0,5	4	0,2	24	2,4	69	0,9
<i>Lanius senator</i>	1	0,03	1	0,1					2	0,02
<i>Lanius minor</i>	1	0,03					1	0,1	2	0,02
<i>Garrulus glandarius</i>	12	0,4	9	0,6	16	0,7			37	0,5
<i>Pica pica</i>	30	0,9	30	1,9	2	0,1	21	2,1	83	1,0
<i>Corvus monedula</i>	13	0,4	1	0,1					14	0,2
<i>Corvus frugilegus</i>			3	0,2					3	0,04
<i>Corvus corone</i>	3	0,1	17	1,1	6	0,3	2	0,2	28	0,3
<i>Corvus corax</i>					4	0,2			4	0,05
<i>Oriolus oriolus</i>	3	0,1					1	0,1	4	0,05
<i>Parus major</i>			1	0,1					1	0,01
<i>Cyanistes caeruleus</i>			1	0,1					1	0,01
<i>Hirundo rustica</i>					1	0,05	1	0,1	2	0,02
<i>Delichon urbicum</i>					1	0,05			1	0,01
<i>Melanocorypha calandra</i>			45	2,9	4	0,2	3	0,3	52	0,6
<i>Calandrella brachydactyla</i>	4	0,1	1	0,1	3	0,1	1	0,1	9	0,1
<i>Galerida cristata</i>	2	0,1	3	0,2	1	0,05	1	0,1	7	0,1
<i>Lullula arborea</i>	6	0,2	1	0,1	4	0,2	1	0,1	12	0,1
<i>Alauda arvensis</i>	11	0,3	8	0,5	15	0,7	6	0,6	40	0,5
<i>Sturnus vulgaris</i>	13	0,4	3	0,2	3	0,1	20	2,0	39	0,5
<i>Pastor roseus</i>	4	0,1							4	0,05
<i>Acrocephalus arundinaceus</i>			1	0,1			1	0,1	2	0,02
<i>Acrocephalus</i> sp.	2	0,1							2	0,02
<i>Sylvia crassirostris</i>	2	0,1							2	0,02

Table 3. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N	Total N	% N
<i>Sylvia nisoria</i>	2	0,1	1	0,1	1	0,05			4	0,05
<i>Sylvia borin</i>	1	0,03							1	0,01
<i>Sylvia atricapilla</i>	1	0,03			1	0,05	2	0,2	4	0,05
<i>Sylvia communis</i>							1	0,1	1	0,01
<i>Sylvia sp.</i>	3	0,1	2	0,1			1	0,1	6	0,1
Sylvidae gen.	1	0,03	2	0,1			2	0,2	5	0,1
<i>Turdus merula</i>	45	1,4	23	1,5	53	2,4	31	3,1	152	1,9
<i>Turdus pilaris</i>	1	0,03							1	0,01
<i>Turdus iliacus</i>	2	0,1	1	0,1	1	0,05			4	0,05
<i>Turdus philomelos</i>	54	1,7	31	2,0	49	2,2	31	3,1	165	2,1
<i>Turdus viscivorus</i>	4	0,1	1	0,1	3	0,1	2	0,2	10	0,1
<i>Turdus sp.</i>	5	0,2	2	0,1	3	0,1	2	0,2	12	0,1
Turdidae gen.	2	0,1							2	0,02
<i>Erithacus rubecula</i>	1	0,03	2	0,1	1	0,05			4	0,05
<i>Luscinia megarhynchos</i>	6	0,2	1	0,1	1	0,05	2	0,2	10	0,1
<i>Saxicola torquata</i>					1	0,05			1	0,01
<i>Oenanthe oenanthe</i>	3	0,1	1	0,1	1	0,05	2	0,2	7	0,1
<i>Oenanthe sp.</i>	4	0,1			1	0,05			5	0,06
<i>Passer domesticus</i>	1	0,03	2	0,1					3	0,04
<i>Passer montanus</i>	1	0,03			2	0,1			3	0,04
<i>Motacilla flava</i>	2	0,1					1	0,1	3	0,04
<i>Fringilla coelebs</i>					1	0,05			1	0,01
<i>Carduelis carduelis</i>					1	0,05			1	0,01
<i>Linaria cannabina</i>							1	0,1	1	0,01
<i>Coccothraustes coccothraustes</i>	6	0,2	1	0,1	1	0,05	3	0,3	11	0,1
<i>Emberiza calandra</i>	10	0,3	14	0,9	6	0,3	15	1,5	45	0,6
<i>Emberiza citrinella</i>	2	0,1							2	0,02
<i>Emberiza cirrus</i>	1	0,03							1	0,01
<i>Emberiza hortulana</i>	1	0,03					1	0,1	2	0,02
<i>Emberiza melanocephala</i>	3	0,1			2	0,1	2	0,2	7	0,1
<i>Emberiza sp.</i>	2	0,1	1	0,1	1	0,05	3	0,3	7	0,1
Passeriformes indet.	8	0,2	13	0,8	11	0,5	11	1,1	43	0,5
Aves indet.	1	0,03	4	0,3					5	0,1
Aves subtotal	1045	32,0	611	39,3	615	28,0	488	48,8	2759	34,4
<i>Ablepharus kitaibelii</i>					1	0,05			1	0,01
<i>Lacerta spp.</i>					1	0,05			1	0,01
<i>Lacerta diplochondrodes</i>			1	0,1					1	0,01
<i>Lacerta viridis</i>	3	0,1			1	0,05			4	0,05
<i>Dolychophis caspius</i>			2	0,1					2	0,02
<i>Zamenis longissimus</i>					1	0,05			1	0,01
<i>Elaphe sauromates</i>					1	0,05			1	0,01
<i>Natrix tessellata</i>			2	0,1					2	0,02
<i>Natrix natrix</i>			1	0,1					1	0,01
<i>Natrix sp.</i>			4	0,3	3	0,1			7	0,09
Reptilia subtotal	3	0,1	10	0,6	8	0,4			21	0,3
<i>Pelobates syriacus</i>	64	2,0	143	9,2	68	3,1	33	3,3	308	3,8

Table 3. (continued)

Prey	NG29 N	% N	MG64 N	% N	MG87 N	% N	MH92 N	% N	Total N	% N
<i>Rana dalmatina</i>	1	0,03							1	0,01
<i>Pelophylax ridibundus</i>	6	0,2	59	3,8	36	1,6			101	1,3
Amphibia subtotal	71	2,2	202	13,0	104	4,7	33	3,3	410	5,1
<i>Potamon ibericum</i>	1	0,03			37	1,7			38	0,5
<i>Pontastacus leptodactylus</i>							3	0,3	3	0,04
<i>Scolopendra</i> sp.	1	0,03	2	0,1					3	0,04
<i>Bradyporus dasypus</i>					1	0,05			1	0,01
<i>Bucephalopectera bucephala</i>	1	0,03	1	0,1					2	0,02
<i>Decticus albifrons</i>	26	0,8	15	1,0	10	0,5			51	0,6
<i>Decticus albifrons/verrucivorus</i>			17	1,1			30	3,0	47	0,6
<i>Platycleis escaleraei/intermedia</i>	2	0,1	2	0,1	1	0,05	10	1,0	15	0,2
<i>Saga natoliae</i>			2	0,1					2	0,02
<i>Tettigonia viridissima/caudata</i>	2	0,1			1	0,05	2	0,2	5	0,1
<i>Tettigonia</i> cf. <i>caudata</i>	5	0,2							5	0,1
<i>Anacridium aegyptium</i>			1	0,1					1	0,01
<i>Calliptamus italicus</i>	1	0,03							1	0,01
<i>Gryllotalpa</i> cf. <i>stepposa</i>	17	0,5	4	0,3	1	0,05			22	0,3
<i>Acinopus</i> sp.	2	0,1							2	0,02
<i>Cerambyx cerdo</i>	7	0,2							7	0,1
<i>Cerambyx</i> sp.	43	1,3	19	1,2	4	0,2	1	0,1	67	0,8
Cerambycidae gen.			1	0,1	1	0,05			2	0,02
<i>Hydrophilus</i> sp.					2	0,1			2	0,02
<i>Copris hipanus</i>			1	0,1					1	0,01
<i>Copris</i> sp.			1	0,1					1	0,01
<i>Lucanus cervus</i>	23	0,7	4	0,3	9	0,4			36	0,4
<i>Oryctes nasicornis</i>	3	0,1	1	0,1			1	0,1	5	0,1
Invertebrates subtotal	134	4,1	71	4,6	67	3,1	47	4,7	319	4,0
Total	3265	100	1554	100	2194	100	1000	100	8013	100

with the only local breeding data of two pregnant females with 4 embryos each in the Maritza River in late December and early January (Özkan 1999).

Predator-prey interactions

Juvenile Coypus fall into the preferred prey weight group of Eurasian Eagle Owls until they reach 1900 g at about 4 months coinciding with their sexual maturity (but not adult size, Sherfy et al. 2006; Lori et al 2013). The invader is a potential prey until the end of its first year having already doubled in weight (Sherfy et al. 2006) comparable to that of some of the owl’s heaviest prey such as the White Stork (*Ciconia ciconia*) (Scherzinger and Mebs 2020). Scavenging by Eurasian Eagle Owls (Milchev and Spassov 2017) may explain older Coypus in owl diets. The small overlap in invader and predator distribution could account the few Eurasian Eagle Owl pairs that preyed on Coypus in the present study. Predation was recorded in a quarter of the

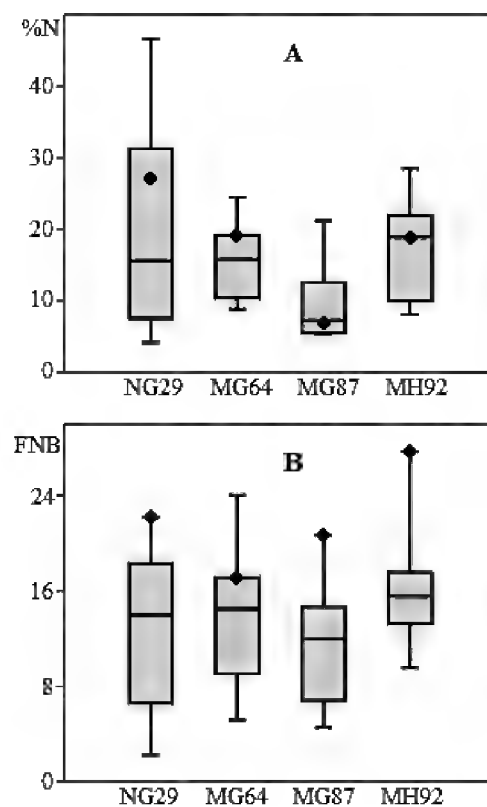


Figure 2. Boxplot of proportions of wetland inhabitants (% by prey number) **A** and food niche breadth (FNB) **B** of Eurasian Eagle Owl (*Bubo bubo*) diets in four breeding territories (UTM squares): rhombs – Coypu-containing diets.

coexistence squares, but without data on the duration of this predator-prey coexistence and the level of overlap of the predator's hunting territory with habitats occupied by the invader. Coypus contributed less than 1% by prey number in the predator's diet similar to Eurasian Eagle Owl studies in the Mediterranean region (Penteriani et al. 2005; Hadad et al. 2022).

Eurasian Eagle Owls opportunistically hunt diverse prey in their permanent breeding territories depending on the available food supply according to the optimal foraging theory (Dalbeck 2003; Penteriani and Delgado 2019; Milchev and Georgiev 2020; Scherzinger and Mebs 2020). Coypus predation did not correlate with the overall increase in the proportion of other wetland inhabitants in the diet of the pairs studied. Therefore, Coypus were not predated as incidental prey in the course of hunting other wetland inhabitants. The single capture of otherwise profitable prey was more likely due to the very low and erratic supply of young Coypus in the hunting territory. This assumption was supported by food niche variation within individual owl localities. The four Coypu-containing diets were among the ones showing the broadest niche-breadth in the respective locality. At the same time, the food niche values in the present analysis fall entirely within the range of the niche values in southeastern Bulgaria (range 1.98 – 34.04, $n = 226$ diets of successful Eurasian Eagle Owl pairs, Milchev and Georgiev 2020).

Targeted research over the past decade (summarized by Koshev et al. 2022) has confirmed the model of Schertler et al. (2020) on the considerable potential of Bulgaria as suitable for Coypu expansion. The low population size of the invader according to

Gruychev (2017) and the present study is confirmed by the few reports of damage in the country (Koshev et al. 2022). The Coypu has been inhabiting protected wetlands near Burgas Bay for more than 25 years (Peshev et al. 2004) without being identified as a biodiversity problem species. Gruychev (2017) and Koshev et al. (2022) indicated periods of low winter temperatures and hunting as factors reducing the numbers of this invasive species, but without specific data. Native predators should be added to these population regulators. While the Eastern Imperial Eagle (Koshev et al. 2022) and Eurasian Eagle Owl are threatened predators listed in the National Red Data Book (Golemanski 2015), the Red Fox (Gruychev 2012) is a widespread common carnivore with a possible invasive suppression potential. There is only scarce data on Coypu as prey for native predators in our country to be properly integrated into future invasive population management and planning in accordance with the EU Invasive Alien Species Regulation (1143/2014) (Smith et al. 2022). Studies in areas of varying Coypu abundance and diversity of predator guilds could determine to what extent conserving predator diversity may contribute to the suppression of populations or to the halt of expansion of this invader. The effectiveness of native predators in naturally suppressing populations of invasive species has already been proven (Carlsson et al. 2009; Nardone et al. 2018; Hernández-Brito et al. 2020; Andreassen et al. 2021).

Acknowledgements

We express our deep gratitude to V. Georgiev, A. Kovachev, M. Chelebiev and G. Rusev for their assistance in the field. We thank J. Menzel for the identification of the bird feathers to species, N. Tzankov for identification of the snake, and D. Chobanov, B. Georgiev and Z. Hubenov for the determination of the invertebrates. Investigations were carried out under grant B-302/1993 of the National Fund for Scientific Research (1994–1996) and with the financial support of J. Menzel in 1998–2013 and H. Frey in 2005. We would like to thank the anonymous reviewers for their valuable comments. The authors declare that this study is in accordance with national legislation.

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